"Investigations into the Segmental Representation of Movements in the Lumbar Region of the Mammalian Spinal Cord." By WILLIAM PAGE MAY, M.D., B.Sc., M.R.C.P., Fellow of University College, London. Communicated by Professor VICTOR HORSLEY, F.R.S. Received July 1, 1896.

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(Abstract.)

Introduction.

The following researches were carried out in consequence of suggestions made to me by Professor Victor Horsley, F.R.S., with the view of throwing light upon the degree to which certain movements, or, speaking more precisely, sensori-motor (kinæsthetic) phenomena are represented in any given segment of the lumbo-sacral region of the mammalian spinal cord, and further of determining what relationship exists between the representation of one movement and that of another. Of methods suggesting themselves for this investigation the one selected was direct excitation of the anterior or posterior roots or of the spinal cord itself.

Historical Introduction.

A series of laborious investigations has been carried out to determine the localisation of certain movements and the physiological relationship of various muscles in and to definite segments of the spinal cord, by Ferrier and Yeo, Bert and Marcacci, Forgue, Sherrington, and Russell, the method of which was limited (controlled by exclusion experiments) to stimulation of the motor roots. I am only aware of one antecedent localisation experiment (by Sherrington) carried out by stimulation of the posterior roots; nor can I find any record of the direct excitation of the surface of the cord for investigating the localisation of movement.

Method of Investigation and Precautions Observed.

(*a*) *Species of Animal.*—The animals chiefly employed were the dog and monkey (*Macacus sinicus* and *rhesus*).

(*b*) *Anæsthetic.*—The narcotic agents used were morphia and ether or, in the monkey, ether alone.

Operative Procedure.

Exposure of spinal cord.

Division of cord and isolation of segments.

The cord was exposed with due observation of well-known precautions (Gotch and Horsley, 'Phil. Trans.,' vol. 182, B, 1891). In some cases the spinal cord and roots were stimulated at first in continuity. In others, before proceeding to experiment, the spinal cord was completely divided at from two to eight segments above the part experimented upon. The spinal roots were divided as detailed in the paper.

METHOD OF EXCITATION.

I. *Electrical.*

Apparatus.—A single Daniell cell was used which supplied a Du Bois Reymond's inductorium of the usual type, the secondary coil being 20 cm. or more from the primary. The electrodes attached to the secondary coil consisted of closely approximated (1 mm.) platinum points. The duration of excitation was, as a rule, momentary, and never exceeded 1—2 seconds.

(*a*) *Excitation of Nerve Roots.*—The nerve roots were raised in the air and the electrodes usually applied, so that the direction of the exciting current was transverse to the nerve fibres.

(*b*) *Excitation of the Spinal Cord.*—The surface of the cord was gently dabbed with small wool swabs, kept in warm saline solution and squeezed dry, before the electrodes were applied. The duration of excitation was always brief, rarely exceeding one second.

The value of the method may be estimated by considering the following facts. On stimulation of the surface of the spinal cord as already mentioned, movement was always elicited in the leg on the side stimulated, when the electrode was applied to the surface of the posterior column, but never, as far as I was able to see, could movement be obtained by the application of this strength or even considerably greater strength of stimulus to the lateral or anterior columns, when adequate precautions (*vide* paper) were taken to prevent the direct spread of the current to the neighbouring root fibres. The movement elicited from stimulating the posterior columns was always marked and quite definite, and merely depended in intensity upon the conditions stated below. For instance, applying the electrodes to the surface of the postero-external column in the fifth lumbar segment of the dog on the left side produced lateral flexion of the spinal column to the same side, flexion and adduction of the hip, flexion of the knee and toes, and movement in the tail (flexion to the same side). But the chief result was the very local effect which could be obtained by varying the point stimulated; thus,

stimulation of a point 1 mm. centrally or laterally to a given point often produced an entirely different resulting movement or no movement at all, which fact is clearly of much importance in showing that, with the above strength of current, the restriction of the stimulus to one point can be accurately attained.

II. *Mechanical.*

As a means of controlling the observations derived from electrical excitation, mechanical stimulation was sometimes employed in examining the nerve roots, and was obtained by pinching the tissues with fine forceps. The results were precisely the same as those gained by electrical stimulation.

On the Results of Direct Excitation of the Surface of the Spinal Cord in the Dog.

I. *Gross Localisation.*

(*a*) *Area Excitable.*—The excitable area of the surface of the cord itself is the postero-external column. Stimulation of the column of Goll produced no movement except in the lower lumbar region, where that column is either very narrow or practically absent, and where, presumably, the effect was due to the stimulus directly affecting the fibres of the postero-external column.

(*b*) *Unilaterality.*—In the large majority (91·5 per cent.) of experiments on animals (dog, cat, monkey) the fact was strikingly evident that the movements produced were limited to the side stimulated.

(*c*) *Vertical Extent of the Spinal Cord in the Dog from which movement in the Lower Limb can be obtained.*—In the dog, movements in the lower limb can be produced from stimulation of Burdach's column from the upper border of the 13th dorsal segment to the lower border of the 1st sacral segment, and from the results obtained it will be seen that the various areas in the postero-external column, the stimulation of which on the surface of the cord produces movements in the limbs, anus, and tail, all overlap one another, but that on the whole the hip area is a little nearer the cerebrum than that for the knee, the area for the knee more proximal than that for the foot, and so on.

(*d*) *Effect of Transversely Dividing the Cord above the Lumbar Enlargement.*—The only effect observed to follow such separation of the cord from the brain, upon the movements elicited as above described, was one of increased excitability. The limits described were found to prevail precisely, and the cord was excitable quite up to the level of the section.

II. *Minute Localisation within the Excitable Area.*

Repeatedly it was found that with a minimal stimulus it was possible to evoke movement either in the tail (and anus) only, or in the hamstrings, or in the hip or in the side only, and whenever this was obtained it was an invariable rule that the point for producing movement in the tail was placed in the cord mesially of that point, stimulation of which gave movement in the hamstrings, and that this latter point was mesial of that for the hip, while most external of all was the point from which movement of the side of the trunk was elicited. This lateral arrangement has been in part foreshadowed by the observations of Mott on the relation between the coccygeal nerves and Goll's column.

Investigation into the Segmental Representation of the Cord by Comparison of the Results of Excitation of the Anterior and Posterior Roots.

(*a*) *Latency of Effect.*—Of course, in accordance with all previous investigations, the delay in passing through the spinal cord was well marked.

(*b*) *Character of Movement Elicited from the Respective Roots.*—Stimulation of the peripheral end of an anterior root gave, on the whole, a quick powerful *extension* of the whole limb, the latency, of course, being extremely short; on the other hand, excitation of the corresponding posterior root resulted in a slower, though strong, *flexion* of the whole limb with a well-marked latency.

This remarkable functional distinction between the roots, viz., anterior giving *extension* and posterior *flexion*, was quite constant, and was obtained in every animal in which the experiment was made. Of course, the movement which took place was a resultant effect, and was produced by the contraction of many muscles, each muscle contracting in whole, or in part, in combination with other muscles to produce the extension or flexion respectively.

The results with each root are given in the tables.

Further, stimulation of a posterior root (say the 5th) produced flexion of a joint or joints even when all the neighbouring anterior roots but one were divided. Hence this flexion can only be due to the stimulus passing from the posterior root through the spinal cord along a particular anterior root to the muscles (differentiation of function in the nerve centre of that root), yet stimulation of this same anterior root produces extension.

And this agrees entirely with the results obtained in a different way by Dr. Risien Russell ('Phil. Trans.,' 1893).

The above experiment also goes to show that stimulation of one posterior root causes impulses to pass out along many anterior roots.

A further important condition of the particular function with which we are now concerned (sensori-motor reflex) is that, from the present investigation, it seems certain that the path along which the impulses pass as evidenced by movement elicited in stimulating a certain posterior root, is directed towards a point *below* the level of that posterior root, and, not as we might suppose, chiefly in the same segment, or even above the level at which the posterior root joins the cord.

The proof of this new conclusion is afforded by many facts given in the paper, not the least interesting of which is, that on direct stimulation of the second or third anterior lumbar roots in the dog, no movement results in the lower limb, yet stimulation of the third posterior lumbar root gives distinct flexion and adduction of the hip and flexion of the knee, and stimulation of the second posterior lumbar root gives slight flexion of the hip and knee. In this connexion also results obtained by Claude Bernard, Schültze, Ramon-y-Cajal, Kölliker, Retzius, and Golgi afford similar evidence.

Influence of the Posterior Roots upon the Nerve Centres in the Spinal Cord.

It was found that repeated excitation of the posterior roots decidedly increased the excitability of the posterior roots themselves, of the spinal cord and of the anterior roots. The difference in the excitability of the preparation before and after the previous stimulation may be represented by the fact that, whereas the minimal stimulus before the application of the repeated stimulus was represented by a distance of 50 cm. of the secondary from the primary coil in the condition of heightened excitability, a minimal stimulus was obtained at a distance of 70 cm. On the other hand, by cooling the posterior roots as suggested by Professor Gad, a converse effect was produced. The results of Belmonda and Oddi are also quoted in this connexion.

Results of Experiments upon the Spinal Cord in the Monkey.

Method.—The same as above.

The same general results were obtained by stimulation of the spinal cord in the monkey as described in the case of the dog. The area found excitable was the postero-external column, stimulation of which from the thirteenth dorsal segment to the second sacral segment inclusive produced after a very short latent period lateral flexion of the spinal column, flexion and adduction of the hip, flexion of the knee, ankle, and toes, movement of the tail and perinœum, and peristalsis (rumbling of the bowels), though it depended on the position of the electrode and the strength

of the stimulus whether only a part or the whole of these movements resulted. Similarly, with regard to the lateral extent of the areas mentioned above, although, of course, a strong stimulus caused movement in all parts named, yet in each case it was quite definite that the area, stimulation of which produced movement in the tail, was nearer the middle line than that for the hamstrings, the area for the hamstrings nearer the middle line than that for flexion of the hip, and this median of that which caused lateral flexion of the side. Hence these results demonstrate from a functional standpoint the anatomical arrangement which has been described by various writers—Ramon-y-Cajal, Kölliker, Golgi, &c.

As in the dog, the knee jerks were found not only present, but even exaggerated, after the cord had been completely divided.

Also section of the cord caused increased excitability of the parts below section, but abolished the movement produced by stimulation of the first or second or third posterior roots below the level of the section, and the more oblique the position of the posterior root fibres in contact with the cord, the greater the interval affected in this manner.

On the Production of Movement by Stimulation of the Anterior and Posterior Spinal Roots in the Monkey.

The general results obtained by excitation of the spinal roots in the monkey were the same as those in the dog. As already known (Sherrington, Risien Russell) stimulation of the third lumbar to the first or second sacral anterior roots (inclusive) alone produces movement in the lower limb, yet, on stimulation of the posterior roots of the twelfth dorsal to the second sacral inclusive, it was found that movement resulted in the lower limb, and in the latter case the bulk of the movement produced is that of flexion.

Summary and Conclusion.

1. *Relationship of Posterior Roots to Reflex Kinæsthetic Centres.*—It appears from the foregoing experiments to be definitely established that any reflex centre derives its chief afferent impulses from a nerve root which enters the cord, as a rule, about two segments higher, *i.e.*, on the cephalic side. This generalisation, established by the method of excitation, is confirmed by anatomical and pathological considerations.

2. *Lateral Arrangement of Fibres in Burdach's Column.*—The fibres of the postero-external column are arranged in a definite and constant order from within out, the innermost fibres (*i.e.*, those nearest the middle line) representing the most distal portions of the tail and lower limb and the outermost the proximal segments of the limbs.

3. Whereas direct excitation of the anterior roots in the dog produces, as a resultant movement, extension of the lower limb, the resultant movement produced from the kinæsthetic centres of excitation of the posterior roots is always flexion. In the monkey there is not this apparent antagonism, because stimulation of the anterior roots in that animal brings out a differentiation of flexion and extension, although excitation of the posterior root gives flexion alone.

"Preliminary Statement on the Development of Sporangia upon Fern Prothalli."

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The observations recorded in this paper were made in the course of an investigation into the relation existing between variability in the fern plant and apogamy in the prothallus. This research was undertaken at the suggestion of Professor Bower, F.R.S., and has hitherto been conducted in the Jodrell Laboratory, Royal Gardens, Kew. To Dr. Bower and Dr. Scott I am indebted for valuable assistance and advice.

In two of the species investigated, *Scolopendrium vulgare*, *L.*, and *Lastræa dilatata*, *Presl.*, sporangia were borne upon the prothallus. In the former they were sometimes associated with apogamous development of the sporophyte, the details of which differ, however, from previously recorded cases of apogamy. As a considerable period must elapse before an amount of material sufficient for the complete study of details of development can be obtained, it appeared advisable to describe the results obtained from the material at present available. Cultures are about to be commenced in the Glasgow Botanic Gardens for the further study of these abnormal prothalli.

The prothalli of the two species investigated will first be described, and the theoretical bearing of the results briefly considered.

Lastræa dilatata, *Presl.*, var. *cristata gracilis*, Roberts.

The spores from which the cultures of this fern were made were obtained from a plant in the collection of Mr. C. T. Druery, F.L.S., who kindly supplied me with material. This variety was found wild in Carnarvon in 1870. Spores were sown in the first week of November, 1895, upon a carefully sterilised soil, consisting of